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# Responses of a Mussel to Shell-Boring Snails: Defensive Behavior in *Mytilus edulis*?

by

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*Abstract.* The mussel *Mytilus edulis* responded to shell-boring snails of the genus *Nucella* with valve gaping, mantle retraction, repetitive valve closures, foot extensions, and changes in byssus attachment rates. Valve closures frequently pinched snails and occasionally displaced them. Repetitive valve closures appeared to force snails away from the valve edges. *Mytilus edulis* attached more byssal threads to adjacent *Nucella* than to adjacent mussels. Attached byssal threads limited snail mobility and sometimes completely immobilized snails. When the foot of a *M. edulis* came into contact with *Nucella,* the snail tended to move. In addition to moving, snails responded to contact by a *M. edulis* foot with shell lifting, shell twisting, and radula strikes. A carnivorous snail that does not bore and two herbivorous snails did not elicit gaping in *M. edulis,* nor did another mussel, *M. californianus,* stimulate shell lifting or shell twisting by *Nucella.* Several alternative hypotheses may explain the behavioral responses of *M. edulis* to *Nucella*: (1) the responses are reactions to a paralyzing substance liberated by the snail, (2) they are shell-cleaning behaviors stimulated by the presence of the snail on the mussel's valves, and (3) they are defensive, anti-predator behaviors. The responses of *M. edulis* to *Nucella* appear most consistent with an anti-predator interpretation of their function.

## INTRODUCTION

Bivalves are vulnerable to shell-crushing, prying, and piercing predators such as crabs, seastars, and snails (SEED, 1976). Within the constraints of the bivalve body plan, which might appear severely to limit behavior, bivalves have diverse behavioral defenses. ANSELL (1969) documented the leaping behavior of several clam species which, when stimulated by seastars, rapidly extend their foot and lift themselves off the substratum. LAWS & LAWS (1972) found that the clam *Donacilla* responds to a burrowing gastropod predator by crawling to the surface. Scallops repeatedly open and close their valves when stimulated by seastars, thus expelling jets of water sufficient to produce a type of swimming (FEDER & CHRISTENSEN, 1966).

In contrast to these bivalves, mussels have been thought to have no such defenses (FEDER, 1972). KIM (1969) observed that the mussel *Mytilus edulis* exhibited no behavior other than a prolonged closure of its valves when attacked by the seastar *Asteria amurensis*. NIELSON (1975) similarly observed only prolonged valve closure when *M. edulis* was attacked by the predatory gastropod *Buccinum undatum*. However, a more recent observation indicates that shell-boring snails stimulate *M. edulis* to perform valve movements, prolonged foot-extensions, and attachment of byssal threads to the snails' shell. These responses have been interpreted as defensive behaviors by WAYNE (1980, abstract). MCCONNAUGHEY & ZOTTOLI (1983) similarly interpreted behaviors of *M. edulis* filmed by Wayne. While the claim of a behavioral defense in *M. edulis* has not been confirmed, such is consistent with bivalve behavior and ecology.

The purpose of this paper is to describe the previously identified behaviors of *Mytilus edulis* (WAYNE, 1980, abstract) and to test for an association between those behaviors and stimulation by shell-boring gastropods.

## MATERIALS AND METHODS

### Preliminary Observations

Experiments were done following several years of preliminary observations, begun in 1976, during which time the responses of thousands of mussels and hundreds of snails were viewed. Descriptions and diagrams of behavior were assembled from observations, photographs, and motion picture films of mussels and snails interacting in aquaria under a variety of conditions.

Experimental mussels and snails were collected at Cape Arago, the Siuslaw Marina, Pirate's Cove, and the south jetties of Coos and Siuslaw bays. These collection sites are within 80 km of the Oregon Institute of Marine Biology (Charleston, Oregon), where the observations and experiments were conducted. Running seawater was provided in all set-ups; seawater temperatures did not exceed ocean temperatures by more than 2°C. All mussels were *Mytilus edulis* Linnaeus, 1758.

### Gaping Response of Mussels Exposed in Aggregate to Free-Moving Snails

A clump consisting of 200–300 *Mytilus edulis* was placed in a 10-gal. (38-L) aquarium. After the mussels attached byssi and the clump had stabilized, 30–40 snails, *Nucella emarginata* (Deshayes, 1839) and *N. lamellosa* (Gmelin, 1791) (formerly placed in *Thais*), were introduced into the aquarium. A 16-mm Bolex camera with a close-up lens was used to film the activity on the surface of the clump at 1 frame per 8 sec. The film was repeatedly viewed at regular speed in both forward and reverse motions by projecting the image on a large sheet of paper. The positions of mussels were drawn on the paper, and the paths of snails were traced to obtain counts of mussels in each of two categories: mussels touched by snails and mussels not touched by snails. For each category, mussels gaping and mussels not gaping were counted. Mussels were judged to be gaping when their valves appeared to be open twice as wide as the valves of adjacent mussels. The results were entered into a 2 × 2 contingency table and the *G*-statistic (Sokal & Rohlf, 1969) was used to test for independence.

### Gaping Response of Mussels Tested Individually

Forty numbered finger bowls (10.5 cm diameter × 4.5 cm) were haphazardly interspersed in a water table. Two mussels (2–3 cm long) were placed in each finger bowl and were left undisturbed for 4 h. After this acclimation period the mussels in 20 of the finger bowls were stimulated with the smooth tip of a glass rod; the remainder were stimulated by contact with *Nucella emarginata*. Stimulation consisted of light touches to the posterior region of the mussel's mantle and valve edges. Each mussel was touched a total of 15 times at intervals of approximately 1 min with either the glass rod or a snail. Touches with snails were accomplished by holding a snail slightly out of water until it extended its foot; then the extended foot was brought into contact with a mussel. Mussels gaping and those not gaping after 15 touches were tabulated for each category of stimulation. The results were analyzed using the *G*-statistic as indicated above.

### Byssus Production by Mussels Stimulated with *Nucella emarginata*

At the conclusion of the experiment described above, byssi produced by the glass-rod-stimulated mussels and the snail-stimulated mussels were counted. Mussels producing one or fewer byssi were discarded, leaving 29 mussels in each set (one extra mussel was chosen at random and excluded to make both sets equal). These mussels were returned to the water table for 12 h, after which time the byssi were counted again. The production of new byssi in the two sets of mussels was tested for similarity (one-tailed) with the Wilcoxon two-sample test (Sokal & Rohlf, 1969).

### Choice Between Mussel and Snail Shell Substrata for Byssus Attachment

Seventy mussels (2–3 cm long) were placed in individual, small finger bowls (8 cm diameter × 3 cm) which were haphazardly distributed in a watertable. Four hours later, 50 of the most firmly attached mussels were stimulated by *Nucella emarginata* (stimulation was as previously described). A plastic grid (1-$cm^2$ openings) was placed over each mussel's finger bowl; then, one new non-stimulated mussel and one *N. emarginata* were wedged into the grid openings. The grid was positioned so that both the inserted mussel and snail were in comparable proximity to the attached mussel below. Each mussel and snail inserted into the grid was chosen and placed so as to provide approximately equal surfaces extending down from the grid into the finger bowl. These setups were returned to the watertable where they remained undisturbed for 12 h, after which time the byssal threads attached to each substratum choice (the mussel and the snail inserted into the grid) were counted. Because the mussels had a third choice of attachment (the finger bowl) that was likely to be selected because of greater area and closer proximity, outcomes in which mussels failed to attach at least one byssal thread to a test substratum were excluded in order to minimize this potentially confounding effect. There were 12 such results. Seventeen more of the original 50 setups were not acceptable for counting owing to mussel escape, snail escape, and dislodgment of the grid. The frequencies of byssal thread attachment to the two substrata were tested for similarity (one-tailed) with the Wilcoxon two-sample test.

### Specificity of the Gaping Response

Mussels secured to a substratum by byssi may have different orientations and can move. It is difficult to stimulate such mussels equally or apply consistent criteria for interpreting their responses. To improve upon this situation, a method for immobilizing mussels was devised. One valve was lightly filed to produce a small flat spot, a drop of cyanoacrylate glue was placed on the flat spot, and the mussel was held against a plastic slide until firmly attached. The slide was then inserted into a slot (with the posterior valve edges upright and the valve opening facing the experimenter) in a specially constructed plastic carriage. The mussels remained out of water for 30–60 min during preparation. The entire carriage with a set of mus-

sels (3.0–4.5 cm long) so prepared was lowered into a 5-L chamber. Control mussels were placed near the chamber's seawater inflow (upstream from the experimental mussels) to avoid stimulating them with water-borne substances that might emanate from the snails or from the experimental mussels. Mussels that showed signs of damage or that failed to open their valves and resume their normal behavior during a period of acclimation were discarded.

Gaping was defined to include both a visible increase in the valve opening and a simultaneous mantle retraction. Stimulation was carried out as previously described. Each experiment included a negative control (stimulation by glass rod) and a positive control. *Nucella emarginata* was used as the positive control in the first experiment; in subsequent experiments, *N. lamellosa* was used because it was easier to handle. In addition to testing *N. lamellosa* in the first experiment, four other snail species, *N. canaliculata* (Duclos, 1832), *Searlesia dira* (Reeve, 1846), *Tegula funebralis* (A. Adams, 1853), and *Calliostoma ligatum* (Gould, 1849), were tested for their ability to stimulate gaping. Mussels gaping and those not gaping after 15 stimulations were tabulated. The data from each experiment were tested for independence with the *G*-statistic.

### Valve Opening, Mantle Retraction, Valve Closures, and Foot Extension in Mussels Stimulated by *Nucella emarginata*

Mussels used for these experiments were 3.0–4.5 cm long, and were immobilized on plastic slides and prepared in a manner similar to that described above. Valve openings and mantle retractions were measured at the posterior valve edges using a small section of plastic ruler held with a long pair of forceps. Mantle retractions to the inside of the valves were recorded as negative numbers (that is, they were considered negative extensions). Valve closures were recorded as observed. Foot extensions and retractions were voice recorded on an audio tape recorder. The time that a mussel's foot remained extended from the valves was then obtained by review of the tape. After 30–40 min into the experiment, experimental mussels were intermittently stimulated for about an hour with *Nucella emarginata*. Stimulation was administered as previously described. Data were recorded before, during, and after the period of stimulation. Another set of mussels prepared in the same manner was used to control for time-dependent variables; these mussels were not stimulated.

Data were collected in five separate trials, each with four to six mussels. There were small time differences (10–30 min) in the pre-stimulation periods among the first few trials. Valve closures and foot extensions were not recorded in the first two. Furthermore, some foot-extension data were lost. All mussels for which both before and after data were obtained were used in the statistical analysis. Paired sets of before and after values for valve opening, mantle retraction, valve closure, and foot extension were tested for equality in a paired analysis of variance (Sokal & Rohlf, 1969). The before values were means of measurements made in the time period before stimulation began. The after values were means of measurements from an equivalent time period immediately after stimulation ended.

Some of the above data consisted of uninterrupted records of sets of valve opening, mantle retraction, valve closure, and foot extension measured during the pre-stimulation period and continuing until several hours after stimulation ended. The data in these sets were combined and plotted to provide a visual illustration of the mussels' responses.

### Shell Lifting and Shell Twisting in *Nucella emarginata*

Individuals of *Nucella emarginata* were filmed at 1 frame per 4 sec while they were stimulated by contact with a freshly excised mussel foot; this was followed, after a 5-min wait, by a second period of stimulation with the foot of a second mussel species. The mussels used were *Mytilus edulis* and *M. californianus* Conrad, 1837. The order of stimulation was randomly varied to control for order dependence. The anterior region of the snail's foot, near the siphon, was touched repeatedly with a mussel foot for 3 min.

In order to keep the snails in front of the camera, the snail's shell was lightly filed and glued (with cyanoacrylate) to the end of an acrylic rod, which was inserted into a hole in the top of a 2-L acrylic filming chamber, thus suspending the snail from the end of the rod into the seawater below. A small plastic sphere (2.5-cm diameter) was brought into contact with the snail's foot, providing a surface upon which the snail could "move." Snails invariably accepted this surface and began rotating the sphere with their crawling motions.

Frame-by-frame analysis was done by placing the 16-mm film over a stage micrometer and viewing the backlighted image at ×25. The vertical distance from the lower edge of a snail's shell to the lowest part of its foot was measured directly on the film. The mean of 10 randomly chosen frames was used to estimate the shell-lifting response of each snail. Responses to each type of stimulation (*M. edulis* foot vs. *M. californianus* foot) were tested for significance in a paired analysis of variance (Sokal & Rohlf, 1969).

The maximum horizontal displacement of the snail's tissue was also measured directly from the film to obtain an estimate of shell twisting. Because a twisting snail will alternately show front and side views (differing in width), the mean difference in tissue width between successive, randomly chosen frames (10 frames were chosen at random and then arranged in ascending order) was used for the estimate of shell twisting. The responses to the two types of stimulation were compared in a paired analysis of variance as indicated above.

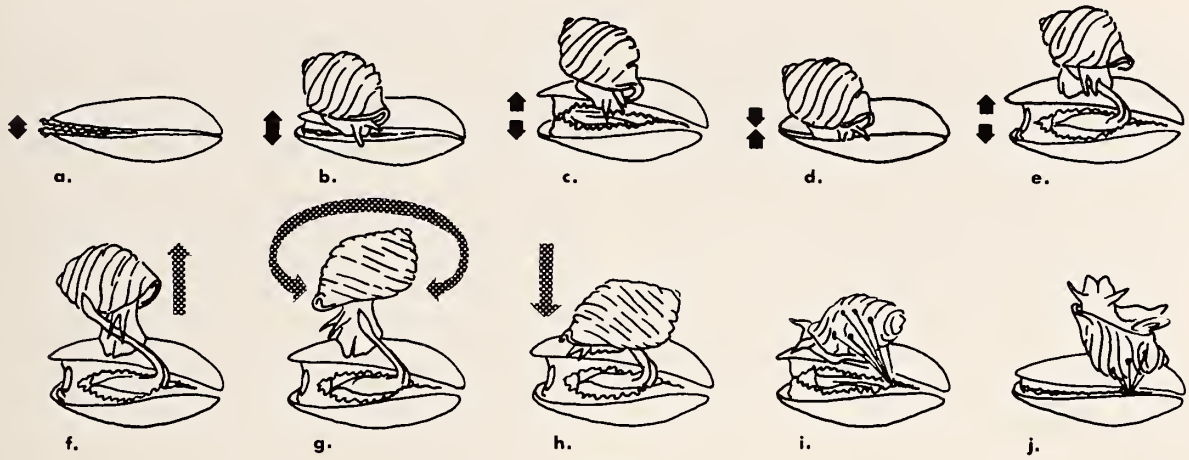


Figure 1

Behavioral interactions between the mussel *Mytilus edulis* and a shell-boring snail of the genus *Nucella*. This sequence (drawn from still photographs and motion picture film) illustrates behaviors that occurred when snails moved freely among mussels. The dark arrows indicate mussel valve movements; the light arrows indicate snail shell movements. a. Undisturbed appearance of *M. edulis*. b and c. Valve opening and mantle retraction following contact by *Nucella*. d. Valve closure on *Nucella* foot. e to h. Mussel foot activity and snail shell lifting and shell twisting. i. Byssal threads attached to the snail. j. Snail immobilized by attached byssus. In addition to the events illustrated here, the snail may be displaced, it may leave its prey, or it may drill and consume the prey.

## RESULTS

### Preliminary Observations and Descriptions

The interactions between *Mytilus edulis* and *Nucella* included behaviors that differed in kind and degree from those observed for mussels or snails alone (Figure 1). Undisturbed mussels kept their valves slightly open and extended their mantle just beyond the valve edges (Figure 1a). Mussels did not react to many organisms that crawled across their valves, nor did they react when their mantle was gently touched with a glass rod. They did, however, retract their mantle and close their valves when strongly prodded; and, even when undisturbed, they closed their valves at intervals.

In contrast, mussels gaped widely after contact with shell-boring snails; the gape was so extreme and the mantle so strongly retracted that much of the mussels' internal anatomy could be seen (Figures 1b, c). Initial contact with a snail usually produced a momentary valve closure; then, the valves gradually opened, increasing until an extreme gape was produced. This condition resembled that of a dead mussel; yet, gaping mussels reacted to contact and, once the snails were removed, gradually returned to their undisturbed appearance.

In addition to gaping, mussels increased their foot activity, and they also exhibited intermittent, repetitive valve closures (the valves closed without any apparent stimulus and then reopened within seconds) following contact with shell-boring snails. Snails crawling near a mussel's valve edges were sometimes pinched and subsequently moved away (Figure 1d); some snails fell off when the mussel's valves closed.

Unlike the stereotyped patterns of gaping and valve closures, foot activity was varied and complex. A mussel might extend its foot over its valves or reach beneath them as though exploring. Contact with a snail often resulted in probing and wiping of the snail's shell and soft tissue (Figures 1f, g, h). Snails responded to such contact by moving away, by lifting and twisting their shell (Figures 1f, g, h), or by directing radula strikes toward the mussel's foot.

Mussels also attached byssal threads to snails. On occasion, a snail's twisting motions broke recently attached threads. The majority of snails placed into aquaria with large clumps of mussel were eventually immobilized by byssi or found with broken byssal threads attached to them. Some snails were found with so many attached threads that it is doubtful they could have pulled free (Figure 1i). Furthermore, many of the immobilized snails were positioned with their foot upward (Figure 1j), and appeared unable to grasp either mussel or substratum.

### Gaping Response of Mussels Exposed in Aggregate to Free-Moving Snails

Ninety-four individual mussels could be seen well enough on the 16-mm film to be counted (Table 1). Of those that had been incidentally touched or crawled over by snails during the filming, 27 were judged to show valve gaping. Of the mussels that were observed to have no contact with

Table 1

Results of two experiments testing for independence of the gaping response in *Mytilus edulis*. The results of the first experiment show counts taken from a film record in which incidental snail contact was observed and subsequent gaping recorded. The snails were *Nucella emarginata* and *N. lamellosa*. The second experiment compares gaping in mussels individually touched 15 times with either a glass rod or *N. emarginata*.

| Treatment | Not gaping | Gaping | *G*-statistic |
|---|---|---|---|
| Experiment 1 | | | |
| No snail contact | 24 | 0 | |
| Snail contact observed | 43 | 27 | 15**** |
| Experiment 2 | | | |
| Touch by glass rod | 40 | 0 | |
| Touch by *N. emarginata* | 19 | 21 | 31.3**** |

**** = $P < 0.001$.

snails during the filming, none gaped. The probability of the null hypothesis that gaping in *Mytilus edulis* is independent of contact with the snails (*Nucella* spp.) is low ($P < 0.001$) and the null hypothesis can be rejected.

## Gaping Response of Mussels Tested Individually

Stimulating mussels with a glass rod produced no valve gaping; by comparison, over half the mussels stimulated with *Nucella emarginata* gaped (Table 1). Again, the probability that gaping is independent of the stimulus is low ($P < 0.001$).

## Byssal Thread Production by Mussels Stimulated with *Nucella emarginata*

Mussels initially stimulated by contact with *Nucella emarginata* produced fewer byssal threads (5.2 per mussel) during a subsequent 12-h period than mussels that were similarly stimulated with the tip of a glass rod (8.1 per mussel). The two sample distributions differed significantly ($n = 58$, $t = 1.86$, $P < 0.05$), and the hypothesis that byssus production is unaffected by the stimulus can be rejected.

## Choice Between Mussel and Snail Shell Substrata for Byssus Attachment

Mussels initially stimulated by contact with *Nucella emarginata* attached more byssal threads during a subsequent 12-h period to live *Nucella emarginata* (2.8 per mussel) than to live *Mytilus edulis* (1.3 per mussel). The two sample distributions differed significantly ($n = 42$, $t = 2.19$, $P < 0.025$) and the hypothesis that mussels will attach the same number of byssal threads to nearby *N. emarginata* as to nearby *M. edulis* can be rejected. On the other hand, at the conclusion of the experiment many *Nucella* were found with their foot gripping the experimental mussel. This result changed the original conditions of the experiment, which provided the experimental mussels with equal proximity to both substrata.

Table 2

Five different gastropods and their effect on gaping in *Mytilus edulis*. Touches with a glass rod were used for the negative control. The positive control was *Nucella emarginata* in the first experiment and *N. lamellosa* in the remainder. Stimulation is described in the text.

| Treatment | Not gaping | Gaping | *G*-statistic |
|---|---|---|---|
| Experiment 1 | | | |
| Negative control | 36 | 0 | |
| *N. lamellosa* | 0 | 36 | 135.8**** |
| Positive control | 0 | 34 | |
| Experiment 2 | | | |
| Negative control | 24 | 0 | |
| *N. canaliculata* | 0 | 24 | 91.6**** |
| Positive control | 0 | 24 | |
| Experiment 3 | | | |
| Negative control | 19 | 1 | |
| *Searlesia dira* | 19 | 1 | 81.4**** |
| Positive control | 0 | 20 | |
| Experiment 4 | | | |
| Negative control | 30 | 0 | |
| *Tegula funebralis* | 32 | 0 | 101.3**** |
| Positive control | 1 | 27 | |
| Experiment 5 | | | |
| Negative control | 20 | 0 | |
| *Calliostoma ligatum* | 19 | 1 | 58.7**** |
| Positive control | 0 | 16 | |

**** = $P < 0.001$.

## Specificity of the Gaping Response

Each of the five experiments testing different gastropods for their ability to produce gaping gave highly significant results (Table 2), in part because of the distinctive contrasts provided by the positive and negative controls. From a total of 126 mussels stimulated with the positive control (*Nucella* spp.), 125 produced a gape; whereas, only one mussel was judged to gape out of 130 stimulated with the negative control (glass rod). Each test of a gastropod's ability to produce gaping can be evaluated by inspecting Table 2 and comparing the snail's effect with that of the positive and negative controls.

In the first experiment, the effect of *Nucella lamellosa* was the same as the positive control. In the second experiment, the effect of *N. canaliculata* was the same as the positive control. In the last three experiments, the effects of *Searlesia dira, Tegula funebralis,* and *Calliostoma ligatum* were the same as the negative controls.

### Valve Opening, Mantle Retraction, Valve Closure, and Foot Extension in Mussels Stimulated by *Nucella emarginata*

Valve opening and mantle retraction were initiated in *Mytilus edulis* immediately after contact with *Nucella emarginata*. When both attributes are plotted on the same graph (Figure 2A), they provide a distinctive "fingerprint" of the gaping behavior. The magnitude of the gaping decreased when stimulation ceased, and it returned to pre-stimulation values after several hours. Foot extensions were more frequent and prolonged after 30–40 min of stimulation; they continued long after stimulation ended (Figure 2B). Valve closures exhibited a similar latent response to stimulation; they also continued long after stimulation ended (Figure 2C).

Statistical analyses of the complete data set (not the subset used for illustration and discussed above) show that before and after values for the experimentals are significantly different (Table 3) for valve opening, mantle retraction, valve closures, and foot extension time. There were no significant time-dependent changes in the control values compared over the same period as the experimentals (valve opening, $n = 11$, $F = 0.32$, $P > 0.5$; mantle retraction, $n = 11$, $F = 1.32$, $P > 0.25$; valve closure, $n = 10$, $F = 1.99$, $P > 0.10$; foot extension, $n = 9$, $F = 0.69$, $P > 0.25$). Assuming this was also true of the experimentals, the hypothesis that *Mytilus edulis* behavior is the same before and after contact by *Nucella emarginata* can be rejected.

### Shell Lifting and Shell Twisting in *Nucella emarginata*

*Nucella emarginata* lifted its shell significantly higher above the substratum ($P < 0.005$) when stimulated by a *Mytilus edulis* foot than when stimulated by a *M. californianus* foot. The mean change in the snail's horizontal displacement was also significantly greater ($P < 0.025$) when stimulated by a *M. edulis* foot than when stimulated by a *M. californianus* foot (Table 4). The hypothesis that *N. emarginata* responds similarly to foot contact by *M. edulis* and by *M. californianus* can be rejected.

## DISCUSSION

By themselves, the behaviors of *Mytilus edulis* reported in this paper are not unusual. Similar results are easily explained and are probably commonly observed. For example, one could expect mussels to attach byssi to snails by chance alone. Furthermore, both byssus production and foot activity probably increase while mussels periodically re-attach themselves to the substratum. Mussels are known to close their valves in response to chemicals (Davenport, 1977), and they may also close them following physical disturbance. Some mussels gape on exposure to air (Lent, 1968), and mussels might be expected to gape when in water with low oxygen. Because bivalves have hinges that exert a tension to open, mussels will also gape as a result of death, or perhaps injury.

However, such explanations fail to account for the present observations. Gaping behavior of *Mytilus edulis* occurred following contact with the shell-boring gastropods *Nucella emarginata, N. lamellosa,* and *N. canaliculata*. Gaping was not produced by contact with a glass rod, with a predator that does not bore (*Searlesia dira*) or with the herbivorous gastropods *Tegula funebralis* and *Calliostoma ligatum*. Mussels, whether attached by their own byssi or glued to plastic slides, gaped in response to snails of the genus *Nucella*. Although limited in extent, these results suggest that gaping is a reaction to stimuli associated with shell-boring gastropods. Additional observations of a preliminary nature indicated that three more shell-boring snails, *Ceratostoma foliatum, Ocenebra interfossa,* and *O. lurida,* stimulated gaping, while additional snails that do not bore, *Olivella biplicata, Lirularia succincta,* and *Amphissa* sp., did not. Furthermore, two East coast shell-boring snails, *Nucella lapillus* and *Urosalpinx cinerea,* stimulated gaping in East coast *Mytilus edulis* (P. Frank, personal communication).

Gastropods generally have well-developed chemosensory abilities (Croll, 1983), and one should expect sessile prey to respond to such olfactory searching predators by closing (Palmer *et al.,* 1982). Consequently, the fact the *Mytilus edulis* gaped in the presence of *Nucella* suggests that the mussel was affected by a toxic or paralytic substance. A choline ester that slows muscle contraction has been isolated from the hypobranchial gland of *N. emarginata* (Bender *et al.,* 1974). The barnacles *Balanus glandula* and *Chthamalus* sp. gape when attacked by *Acanthina punctulata,* and the gape has been linked to toxins from the snail's hypobranchial gland (Sleder, 1981). Perhaps the repetitive valve closures of *M. edulis* help remove such substances by increasing water exchange. However, interpreting *M. edulis* gaping as a reaction to snail toxins is inconsistent with several other observations suggesting that gaping mussels are not vulnerable to attack: gaping *M. edulis* closed their valves when their soft-tissue was touched by either a snail or a glass rod; gaping mussels increased their foot activity; *Nucella* frequently abandoned mussels that were gaping; and *Nucella* did not feed on live mussels through their gaping valves during any of the hundreds of gapes observed in these experiments, nor are *Nucella* known to do so from any reports in the literature. Furthermore, no gaping was observed in *M. californianus* during preliminary observations of about 30 individuals stimulated by *Nucella.*

The gaping behavior, then, presents a contradiction. This contradiction could be resolved by one of several possibilities. First, gaping might be an incidental response to substances in *Nucella* that paralyze other prey. Second, *Nucella* may induce gaping and then sample mussels to test their suitability as prey. Third, because choline esters are known to stimulate escape and avoidance responses (literature cited by Croll, 1983), defensive behavior is

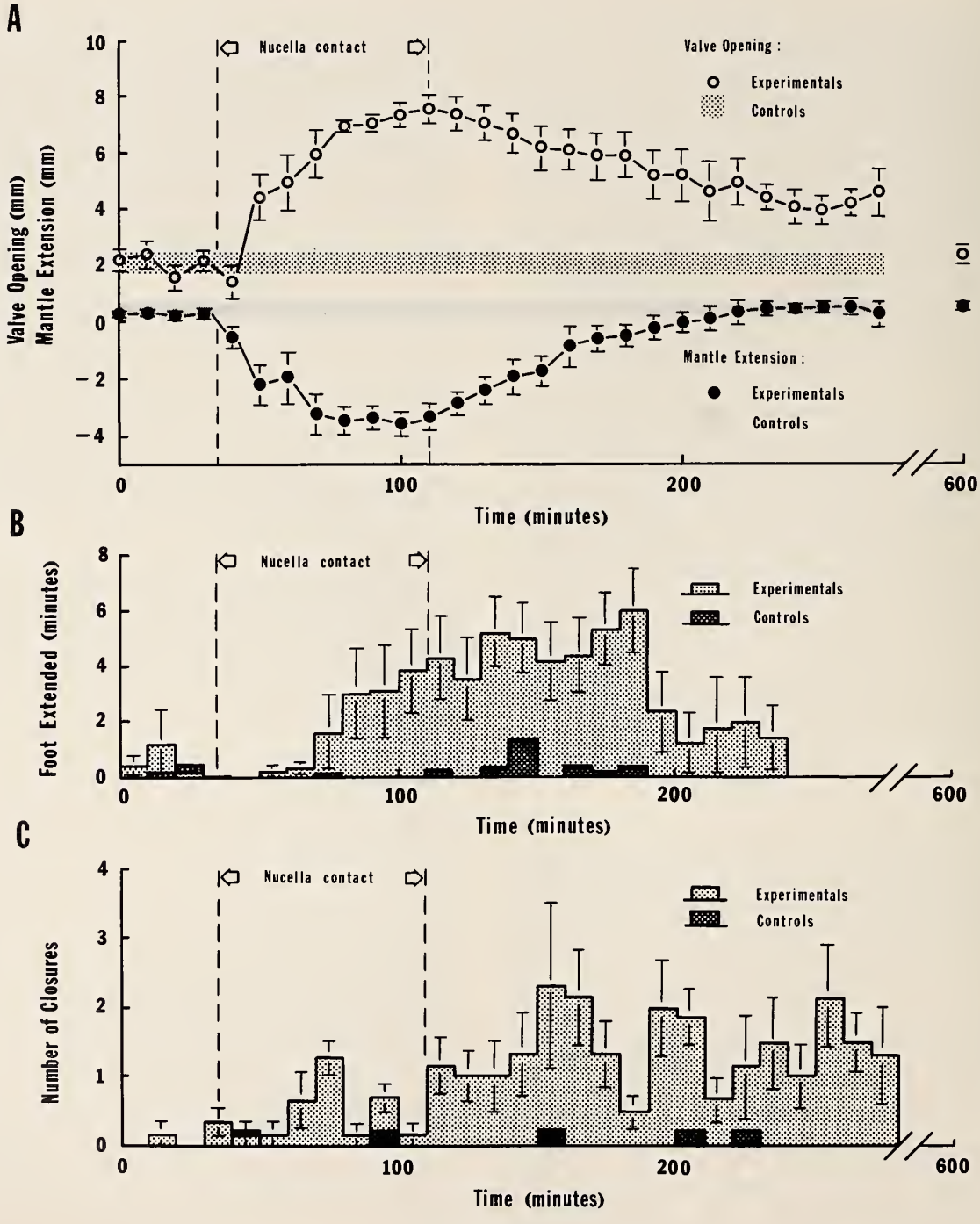


Figure 2

Temporal changes in the behavior of *Mytilus edulis* as a function of contact by the shell-boring snail *Nucella emarginata*. The values plotted are the means from 6 experimental and 5 control mussels. The vertical bars represent ±1 S.E.; however, note that these data are a subset of those used for significance testing and are themselves not suitable for such. See text for further information. A. *Gaping*. The gaping behavior includes valve opening and mantle retraction (mantle retractions are plotted as negative mantle extensions). The control data are shown as gray bands to better illustrate the gaping behavior; actual control data points match the pre-stimulation values of the experimentals. B. *Foot activity*. Time in minutes that a mussel foot extended outside the valves during each 10-min period. C. *Valve movements*. Number of valve closures during each 10-min period.

Table 3

Results of paired analyses of variance used to test for changes in valve opening ($n = 10$), mantle extension ($n = 10$), valve closures ($n = 9$), and foot extension ($n = 8$) in *Mytilus edulis* following contact with *Nucella emarginata*. Means are given for before (pre-stimulation) and after (post-stimulation) data. See text for method of stimulation and information on controls.

| Source of variation | Mean | | df | SS | *F* |
|---|---|---|---|---|---|
| | Before | After | | | |
| Valve opening | 2.9 mm | 6.2 mm | | | |
| Snail contact | | | 1 | 56.1 | 15.4*** |
| Individuals | | | 9 | 42.4 | 1.26 |
| Remainder | | | 9 | 32.8 | |
| Mantle extension | 0.3 mm | −2.4 mm | | | |
| Snail contact | | | 1 | 33.8 | 11.6** |
| Individuals | | | 9 | 21.5 | 0.82 |
| Remainder | | | 9 | 26.2 | |
| Valve closure | 0.2 | 1.2 | | | |
| Snail contact | | | 1 | 4.49 | 8.16* |
| Individuals | | | 8 | 4.57 | 1.04 |
| Remainder | | | 8 | 4.40 | |
| Foot extended | 0.23 min | 1.23 min | | | |
| Snail contact | | | 1 | 32.0 | 10.1* |
| Individuals | | | 7 | 29.8 | 1.35 |
| Remainder | | | 7 | 22.1 | |

* = $P < 0.025$.
** = $P < 0.01$.
*** = $P < 0.005$.

suggested. Palmer *et al.* (1982) suspect that prolonged withdrawal in *Balanus glandula* is a chemically mediated avoidance response. *Nucella emarginata* is one of the predators that elicits the response. It is possible that gaping is an avoidance behavior that obscures information required by *Nucella* for prey identification, or perhaps the gape interferes with the snail's attack by pushing the snail against adjacent substrata. However, if gaping is a mussel defense, then the function of gaping in *M. edulis* is contrary to what is found in barnacles, and ability of *Nucella* to use olfactory information from *M. edulis* is contrary to what is expected.

When one considers how mussel valve movements, foot motions, and byssal thread attachments might affect a shell-boring snail, it is difficult not to conclude that such behaviors increase the snail's time and energy costs. For example, from the standpoint of time and energy, the best place for a snail to drill a mussel is near the valve edges. Yet, snails seldom drill there. The majority of drill holes in mussel valves are found in the thicker central region (Carefoot, 1977). In the present study, snails invariably moved away from the valve edges in apparent reaction to their movement. Perhaps the valve movement forces snails into the central region where more time and energy are required for penetration. Another explanation for the location of drill holes in mussels is that the snails may be attempting to maximize access to the underlying tissues.

Table 4

Shell lifting and shell twisting in *Nucella emarginata* after contact by *Mytilus edulis* and by *M. californianus*. A paired analysis of variance was used to test the responses for similarity ($n = 6$). See text for method of stimulation and details of measurement.

| Source of variation | Mean response of snail when stimulated by | | df | SS | *F* |
|---|---|---|---|---|---|
| | *M. edulis* | *M. californianus* | | | |
| Shell lifting | 0.74 cm | 0.47 cm | | | |
| Mussel foot | | | 1 | 0.33 | 28.4*** |
| Individuals | | | 5 | 0.21 | 3.64 |
| Remainder | | | 5 | 0.06 | |
| Shell twisting | 0.22 cm | 0.05 cm | | | |
| Mussel foot | | | 1 | 0.13 | 10.4* |
| Individuals | | | 5 | 0.09 | 1.5 |
| Remainder | | | 5 | 0.06 | |

* = $P < 0.025$.
*** = $P < 0.005$.

Yet, the snails' possession of an extensible proboscis would seem to relax such a strategy. Furthermore, several other bivalves move their valves in the presence of predators (Carriker & Van Zandt, 1972; Kim, 1969) suggesting a defensive role for valve movement. In addition, Stimson (1970) notes that *Nucella* has a tendency to retract its foot, lose its grip on the substratum, and be washed away when pinched by the shell of the owl limpet, *Lottia gigantea*. *Nucella* behaved similarly when pinched by *M. edulis* valves, again suggesting that valve movements affect the location of drill holes. That such pinches dislodged *Nucella* also suggests a means by which the sessile mussel may "escape" its predator.

The foot motions of *Mytilus edulis* were similar to those previously described by Theisen (1972) as shell cleaning behavior. Shell cleaning involves "licking" motions of the foot, which remove small particles from the valves. A possible explanation for the foot activity of *M. edulis* observed in the present study is that it was shell cleaning behavior, and it was stimulated by presence of *Nucella* on the mussel's valves. On the other hand, several aspects of the foot activity were more suggestive of interference behavior than they were of shell cleaning. First, the foot was frequently extended above the valves; thus, "licking" was not the only behavior observed. Second, several mussels were heavily encrusted with barnacles; consequently, one should expect the stimulus for shell cleaning to be obscured. Third, filing their valves and gluing plastic slides to the mussels did not stimulate shell cleaning. Fourth, the wiping and probing motions of the foot appeared to be directed at the snail; and fifth, the snail frequently moved following contact by the mussel's foot.

*Mytilus edulis* can immobilize *Urosalpinx cinerea* by attaching byssi to the snail's shell. These immobilizations

are not thought to have ecological significance because they occur at temperatures at which bivalves are active but snails have gone into hibernation (CARRIKER, 1981). In the present study, however, *M. edulis* attached byssi to *N. emarginata* and to *N. lamellosa* at temperatures at which both mussels and snails were active. As in the case with *U. cinerea, Nucella* were often immobilized. These observations suggest byssal threads are used defensively, inasmuch as byssus attachment to an active snail could, by restricting the snail's movement, prolong the attack, cause the attack to be aborted, or increase the snail's risk to predators and physical stress. When provided with two substratum choices, *M. edulis* attached more byssal threads to live *Nucella* than to live *M. edulis,* thus indicating that byssus attachment is biased toward the predator. However, this result must be interpreted cautiously because the snails increased their proximity to the mussels during the experiment. On the other hand, such changes in proximity are an inevitable consequence of a snail's attack.

The shell-lifting and shell-twisting behaviors of *Nucella* could defend it from byssus attachment. Byssal threads were broken by such motions, and the same motions probably make byssus attachment more difficult. Similar shell twisting and shell lifting in other gastropods has been interpreted as defensive behavior (CLARK, 1958; FEDER, 1967, 1972; PRATT, 1974). Alternately, such behavior in *Nucella* might be considered a reaction to food, but this argument is weakened by the fact that a second, although not a preferred prey, *Mytilus californianus,* does not stimulate the same behavior.

## CONCLUSIONS

Demographic studies of mussels indicate that they experience heavy predation in most environments. Some mussels have morphological defenses against predation. Greatly thickened valves are associated with resistance to shell-boring gastropods (VERMEIJ, 1978) and such thickened valves are characteristic of *Mytilus californianus.* Horse mussels, *Modiolus modiolus,* produce tapering hairs or awns on their periostracum which discourage attachment by the predatory whelk *Thais lapillus* (WRIGHT & FRANCIS, 1984). Predation pressure is especially severe for *M. edulis;* it is the preferred prey of at least 10 different invertebrate predators and is consumed in large numbers by many of them (SEED, 1969; HARGER, 1972; SUCHANEK, 1978).

Heavy predation by specialized predators should provide strong selection pressure for the evolution of defensive, anti-predator mechanisms; however, *Mytilus edulis,* with its relatively thin, smooth valves, appears to have poor morphological defenses against shell-boring snails. On the other hand, these small, specialized predators stimulate valve movements, foot motions, and byssus attachment by *M. edulis,* all of which could interfere with the snail's selection of a drill site and eventual penetration of the mussel's valve. Several explanations, including toxic secretions from snails and shell-cleaning behavior, may account for such responses in *M. edulis,* but the mussel's behaviors appear more consistent with an anti-predator function. While *M. edulis* seems to have a poor morphological defense, the mussel's responses strongly suggest a behavioral defense. A comparable situation exists for *Tegula aureotincta* (SCHMITT, 1981). Like *M. edulis, T. aureotincta* is a preferred prey with an inferior morphological defense. Significantly, perhaps, *T. aureotincta* utilizes a behavioral defense.

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